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# **The Role of Movement Restrictions in Limiting the Economic Impact of Livestock Infections**

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## **Abstract**

**Movements are essential for the economic success of the livestock industry. These movements however bring the risk of long-range spread of infection, potentially bringing infection to previously disease-free areas where subsequent localised transmission can be devastating. Mechanistic predictive models usually consider controls that minimize the number of livestock affected without considering other costs of an ongoing epidemic. However, it is more appropriate to consider the economic burden, as movement restrictions have major consequences for the economic revenue of farms. Using mechanistic models of foot-and-mouth disease (FMD), bluetongue virus (BTV) and bovine tuberculosis (bTB) in the UK, we contrast the economically optimal control strategies for these diseases. We show that for FMD, the optimal strategy is to ban movements in a small radius around infected farms; the balance between disease control and maintaining 'business as usual' varies between regions. For BTV and bTB, we find that the cost of any movement ban is more than the epidemiological benefits due to the low within-farm prevalence and slow rate of disease spread. This work suggests that movement controls need to be carefully matched to the epidemiological and economic consequences of the disease, and optimal movement bans are often far shorter than existing policy.**

55

56 Recent outbreaks have shown the sensitivity of farming industries to invasion by novel  
57 pathogens, with examples including: the 2001 outbreak of foot and mouth disease (FMD) in the  
58 UK and the Netherlands [1-3]; the 2006-7 outbreaks of bluetongue virus (BTV) to Northern  
59 Europe [4]; the 2014 invasion of Lumpy Skin disease to Greece and the Balkans [5-6]; and the  
60 pan-European spread of Schmallenberg virus since 2011 [7-8]. These recent experiences have  
61 increased fears about novel infections that may threaten livestock industries in disease free  
62 countries in the future, such as avian influenza, african swine fever, Newcastle disease, Rift  
63 Valley fever or brucellosis, in addition to those above. Once established, there are considerable  
64 difficulties in controlling endemic diseases in the livestock industry, as exemplified by infections  
65 in the UK such as Footrot [9], Scrapie [10] and bovine tuberculosis (bTB) [11-12]. Many of these  
66 novel and endemic diseases spread easily between the animals on a farm, which are kept at  
67 relatively high densities, and can spread between farms through a mixture of air-borne infection,  
68 fomites, vector-transmission and animal movements [13]. Of these transmission routes, animal  
69 movements have the potential to lead to very long-distance dispersal of infection, and yet can  
70 be readily prevented through emergency legislation [14]. For this reason, local, regional or  
71 national scale movement restrictions (often banning the non-essential movement of all farm  
72 livestock) are often one of the first control policies to be adopted when an outbreak occurs [15].  
73 Such bans have the advantage (in comparison to say vaccination or other treatments) that they  
74 are independent of disease etiology and therefore can be enacted before the causative agent  
75 has been fully identified.

76

77 The revenue of livestock farms is largely based on the movement of animals, either through  
78 selling animals to other farms or by moving animals to slaughter. Therefore, adopting any form  
79 of movement restrictions may have substantive economic consequences for the livestock  
80 industry. In the UK, a nationwide ban on animal movements and the “closing of the countryside”

during the 2001 FMD outbreak had huge economic implications for the tourist industry and the wider rural economy [16]. Given these extreme financial implications, and that money provides a unified measure for comparing multiple consequences, here we optimise infection control in terms of minimising the economic consequences of any intervention measure. We adopt an aggregate, national economic perspective and consider the total costs of an epidemic and the associated movement controls to both the livestock industry and beyond. In particular we focus on outbreaks of FMD and BTV, and endemic bTB, which offer contrasting behaviour. FMD is characterized by extremely rapid within-farm transmission and localized airborne or fomite spread [2-3]. BTV is a more cryptic infection, often only infecting only a proportion of the animals on a farm and can spread over large distances by infected midge vectors [17]. bTB is a much slower infection, generally infecting just one or two animals on a farm; problems with control are exacerbated by poor test sensitivity [12] and potential reservoirs of infection in wildlife populations [18-19].

Quantifying the economic impact of an animal disease and its management is complex. The economic costs of an outbreak fall into three broad categories: costs due to loss of production, control costs and wider economic costs [20]. The large-scale 2001 UK FMD outbreak provided some of the most comprehensive data available; it is estimated that this outbreak cost the UK livestock sector £3.1 billion with similar additional costs to the wider economy. However, it is acknowledged that these wider costs were more challenging to calculate as losses in one area (e.g. tourism) may have led to gains in other areas of the economy [16]. In addition, economic impacts may depend in a highly non-linear manner on the scale of an outbreak; a short duration outbreak may have a limited impact on farming, whereas a protracted outbreak can leave the industry unable to recover [21].

In the event of livestock disease outbreaks or the management of endemic disease, there are economic trade offs that need to be taken into account when considering a set of control options

[22] and the policy that is deemed to be optimal may be dependent upon specific demographic characteristics and the state of the outbreak as it evolves in time [23-25]. Recently, complex economic models have been developed which capture the multitude of economic interactions that are perturbed by an infectious disease outbreak and the subsequent control measures. These have been used to calculate the economic impact of outbreaks such as FMD in the UK [26] and South America [27], avian influenza in the Netherlands [28] and Rift Valley Fever in Kenya [29]. Here we use a simpler approach in which the cost calculation is comprised of the economic impact on up to five different sectors, linearly dependent on different attributed of each disease. This approach is designed to enable comparisons between different policies and indicate those that are optimal in reducing outbreak costs; we recognise that this is a simplification of the true economic cost of an outbreak, especially if different controls can generate extremes of epidemic size and duration.

In this paper, we use state of the art mathematical models [2,12, 30-31] to investigate the cost-effectiveness of local and regional movement control upon outbreaks of FMD and BTV and the endemic dynamics of bTB in the UK. Such policies, if implemented effectively, could balance the need of containing and controlling the spread of infection with the economic incentive of maximising business continuity for a large number of unaffected farms.

For all three diseases we used sophisticated stochastic spatial simulations, which are matched to historical epidemiological data; these are used to address how costs (including culling, testing, loss of exports and tourism) vary with the scale and nature of movement restrictions. All simulations reflect disease-specific transmission routes and control measures. As such, localized high-risk (dangerous contact) culling is implemented for FMD, a range of movement zones (protection and surveillance zones) are enforced for BTV, while for bTB a targeted test-and-slaughter policy is enacted. Greater information on the formulation of the models is included in the Supplementary Material. These three infections reflect different contributions of

movements to the spread of infection; in the absence of movement controls, the movement of cattle accounts for 28% (26%-31%), 4% (2%-15%) and 13% (7%-22%) for FMD, BTV and bTB respectively (95% confidence intervals are given in brackets).

For a given set of movement controls, we consider five factors that may contribute to the overall national cost of the outbreak: (i) the number (and type) of animals infected, and their eventual fate; (ii) the number (and type) of animals culled as part of the control; (iii) the duration of the outbreak; (iv) the number of movements prevented by the restrictions and (v) the amount of testing that was undertaken (for bTB only). These epidemic descriptors are used to calculate the economic losses to different sectors:

- **Direct costs to farms** are a weighted sum of the number of animals infected or culled.
- Costs due to **Welfare culls** are proportional to the number of farm days (farms × days) where movements are completely banned.
- Costs to the wider **Agricultural Sector** are proportional to the number of animal movements that are prevented by movement restrictions.
- **Loss of Exports** is proportional to the duration of the epidemic plus a delay to achieve disease-free status.
- **Impact on Tourism** is proportional to the number of farm days where movements are completely banned, assumed to give a measure of the regions of the countryside that are closed (FMD only).
- **Testing Costs** (bTB only) are proportional to the number of animals tested, and include both costs to the farmer and those met by government.

The precise formula used to calculate these costs are given in more detail in Table 1 (the implications of changes to each economic value upon the optimal policies can be assessed using the Shiny app: [https://livestockmovements.shinyapps.io/movement\\_control/](https://livestockmovements.shinyapps.io/movement_control/)). We now consider

how movement restrictions of different types can minimise the overall expected economic cost of the disease, as well as which controls minimise economic extremes (as captured by the upper 95th percentiles). In this paper we take a national perspective, minimising the total losses to the country including government, farmers, wider rural economy and tourism where appropriate.

The costs associated with FMD outbreaks differ considerably according to the scale of the movement ban and the origin of the outbreak (figures 1A and B correspond to outbreaks starting in Cumbria and Devon respectively; other regions are shown in the Supplementary Material, Supplementary Figure 1). We consider the outbreak costs from multiple simulations with interventions including culling of livestock on infected premises and on farms considered high-risk (dangerous contacts; [32]), together with a localized movement ban surrounding infected premises. We show by bars the mean total cost (together with 95% confidence intervals) broken down into five key losses; it is clear that direct costs to the farm (dark blue) and impact on tourism (orange) dominate but show opposite trends with the radius of movement control. We also consider extreme ‘worse-case’ costs (red dots) which are defined as the upper 95% prediction interval of all simulations.

For Devon (figure 1B), direct farm costs predominate and the economic optimum occurs at relatively small radius movement bans (12-38 km – horizontal black bar); for radii below this optimum, the scale of potentially extreme ‘worst-case’ costs (red dots) increases and hence small-scale bans are far less effective. Even if the effects of tourism are ignored and we focus only on costs to the whole agricultural sector, there is still an optimal radius although this is increased (42-48 km – horizontal blue bar). Finally, if the main concern is mitigating ‘worst-case’ costs, the optimal radius is larger than when considering the mean (22-48 km – horizontal red bar).



For Cumbria the patterns look subtly different. Due to higher densities of livestock, outbreak sizes and hence direct costs remain relatively high even when movement restrictions are enacted nationally. An implication of this is that the total costs associated with national control are higher than those when there are no movement restrictions: it may be more cost effective to allow all movements rather than ban all movements. For Cumbria the optimal radius for movement bans is more tightly defined compared with Devon where there is more stochastic variability: the optimal ban radius for mean total costs is around 20 km, when tourism costs are excluded this increases to 52-63 km, whilst when mitigating 'worst-case' costs the optimal radius reduces to just 7.5-13 km.

For BTV the potential control options are very different; culling has very little impact and therefore was not used as a practical control measure. In addition, while the 2001 (and 2007) FMD epidemics led to national movement bans, the 2007 BTV outbreak was controlled by the establishment of localised zones around infected areas, where movements from higher risk to lower risk zones were banned. Mirroring this strategy we focus on the optimal generation of three zones: an inner zone with a complete movement ban, a high-risk protection zone (PZ) and an outer lower-risk surveillance zone (SZ). All farms within the inner zone are completely banned from moving livestock either off-farm or on-farm. Livestock movements are not completely restricted for farms within either the PZ or SZ, however livestock could not be moved from a farm in a higher risk zone to a farm in a lower risk zone.

Our results focus on outbreaks initiating in Devon (although results are qualitatively generic; see Supplementary Figure 2 for outbreaks in Suffolk, where the 2007 outbreak started), which are generally larger due to a combination of warmer summers and higher host density necessary for sustained transmission. Figure 1C compares five different radii for the complete movement ban (different colours) and four combinations of protection and surveillance zones (PZ and SZ respectively, x-axis). We consistently find that not having any complete ban (purple)

outperforms all other strategies from an economic perspective, irrespective of the size of the PZ and SZ. In part this is due to rapidly increasing losses due to tourism, to the wider agricultural sector and due to welfare as the number of farms experiencing a complete ban increases; even ignoring tourism these results still hold. When no complete bans take place around infected farms, Figure 1D focuses on the optimal radii for the protection and surveillance zone -- assuming that the SZ radius is twice that of the PZ. For BTV (and assuming no complete bans) it is only the direct costs to farms (blue) and agricultural sector losses (green) that impact on the economic costs. We note that agricultural sector losses increase with the radii of the two zones, but the epidemic size (and hence direct costs to farms) is largely independent of movement bans, leading to the situation where it is optimal to allow free movement of livestock. Our model prediction of ineffectiveness of movement bans in controlling BTV broadly agrees with another UK BTV transmission modelling study [33], where movement bans were found to have a limited impact on controlling farm-to-farm spread even without the ancillary consideration of economic impact.

Finally, for endemic bTB, we consider the impact of a combined movement ban and testing protocol, such that, in addition to the standard (test and cull) policy, once a farm tests positive all surrounding farms within a given radius are also placed under a cattle-only movement ban until they clear a subsequent test within 60 days. As such, waves of testing and cattle movement bans can propagate through highly infected regions. A scenario is also considered where no movement controls are imposed even when infected animals are detected (and culled). We consistently find that this no-movement-ban policy has the lowest economic costs (figure 1E) as it eliminates the costs to the agricultural sector that arise from movement restrictions, and that larger radii bans are increasingly costly. (An alternative policy that only bans movements from infected farms but still generates tests within a given radius, has a local minimum cost at a radius of around 2km; Supplementary Figure 3). The economically optimal policy, however,

leads to a long-term increase in the number of infected cattle (figure 1F), whereas large-radius ban-and-test strategies are predicted to lead to far lower incidence. Importantly we note that there is relatively little difference in incidence between the no-ban strategy and the current policy of only banning movements from infected farms (0km).

The results for both BTV and bTB contrast with the findings for FMD; this may be explained by the different within-farm dynamics of the infections. Given that FMD is directly transmitted and highly infectious, any movement of an infected animal into a naive farm leads to rapid infection of all livestock on the farm, hence movements are extremely detrimental. In contrast, BTV is vector transmitted such that infection can readily escape the farm environment by the movement of vectors. In addition the weakly transmissible nature of both bTB and BTV means that there is only limited saturation (density dependent effects) of infection on farms; this means that the movement of an infected animal simply transfers the risk of infection to animals on the new farm rather than on the farm of origin.

The economic parameters used in this work (Table 1) have been based on government agency assessments of national costs associated with each disease. However, such parameters are open to different interpretations and will be influenced by both the scale of the outbreak and the current economic climate. In addition different organisations may wish to alternative perspectives, by focusing on losses to particular sectors, such as the farming industry or government. This entire range of sensitivity can be explored through the online Shiny app ([https://livestockmovements.shinyapps.io/Movement\\_Control/](https://livestockmovements.shinyapps.io/Movement_Control/)), which allows the individual economic parameters to be varied (although sensitivity to individual economic values is considered in the Supplementary Material – see Supplementary Figure 4). In general we find that the optimal movement ban radius for FMD is most sensitive to the costs of livestock and

tourism losses, while for BTV and bTB the optimal radius only changes at extremes of economic costs.

For a policy of movement bans to be effective, it must be enforceable. There is an argument that a nationwide ban, where all livestock movements are prevented, could be more enforceable as it is more obvious when the ban is being broken. In addition, a regional ban may meet opposition from farmers just within the radius of the movement ban who view themselves penalised relative to farms just outside the radius. However, localised movement bans (of the form instigated during the 2006 bluetongue epidemic) allow resources to be concentrated into a smaller regions, and hence it may be easier to enforce compliance. This may be particularly the case in lower and middle income countries, when typically interventions are initiated at the local level in response to livestock disease outbreaks [33]. Incorporating such factors into mathematical models requires the ability to predict farmer behaviour which is likely to be complex and heterogeneous, and beyond the scope of this work.

This suite of model predictions demonstrate that movement restrictions have a dramatic impact on the national cost of livestock diseases, such that large-scale movement bans are generally prohibitively expensive. By considering these three very different infections, we draw the general conclusion that movement bans are most needed for diseases like FMD, where there is considerable within farm transmission and where movements form a dominant source of long-range transmission. For slower spreading infections, exemplified by bTB and BTV, it may be economically preferable to allow movements to continue unrestricted. Optimisation of movement restrictions, informed by bespoke predictive models, has the potential to dramatically reduce the cost of an outbreak: balancing the need for control and containment with the desire to maintain the economic viability of the livestock industry.



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### **Author Contributions**



MJT, SB, EBP and MW carried out simulations using the three livestock disease models. NB developed the Shiny app for visualisation of sensitivity analysis. MJK and MJT analysed the outputs of the simulation models. MJK led the sensitivity analysis of the modelling results and provided intellectual expertise on all three livestock disease models. All authors contributed to the writing of this manuscript.

#### **Data Availability Statement**

The raw simulation data used to create figure 1 in the main text and all figures in the supplementary material can be made available upon acceptance of this manuscript. The authors do not have permission to share the farm level data for the United Kingdom. However, the demographic data that includes farm locations, farm sizes and species composition, as well as the data on livestock movements between farms can be via the RADAR system by emailing [RADAR@apha.gsi.gov.uk](mailto:RADAR@apha.gsi.gov.uk).

#### **Code Availability Statement**

The code used to create analyse the raw data and produce the figures presented in this manuscript will be made available upon acceptance of this manuscript. The code for the simulation models can be accessed by contacting the relevant contributing author: (i) for the foot-and-mouth disease model, Mike Tildesley; (ii) for the Blue tongue virus model, Sam Brand and (iii) for the bovine Tuberculosis model Ellen Brooks Pollock.

#### **Competing Interests Statement**

The authors declare that they have no competing interests as defined by Nature Research, or other interests that might be perceived to influence the interpretation of the article.

#### **Figure Legends**

**FIGURE 1. Impact of movement bans on the cost of livestock infectious diseases.** Panels A and B show results for FMD epidemics seeded in 5 infected farms in Cumbria and Devon, respectively. Stacked (coloured) bars represent the different costs: direct farm losses, welfare losses, losses to the general agricultural sector, lost revenue due to export bans and the losses to the tourist industry (as quantified in

Table 1). Red points (with confidence intervals from bootstrapping) represent the upper 95% prediction interval on the costs. Horizontal bars show the optimal movement ban radius to minimise different economic measures: black bar average total costs; blue bar average cost without tourism losses; red bar the upper 95% prediction interval. Panels **C** and **D** focus on bluetongue outbreaks initiated in Devon. In **C** we consider the mean outbreak cost, and vary both the inner radius where movements are completely banned (colours) and the Protection / Surveillance zones where only outward movements are banned (grouped on the x-axis). In **D** we focus solely on the Protection / Surveillance zones, using the same format as graphs A and B. Panels **E** and **F** present results for bovine tuberculosis, simulations are run for 14 years with alternative movement controls and testing implemented for the last 6 years, and the costs averaged across all years of alternative control. As in other panels, in **E** we show means, extremes and the associated confidence intervals. In **F**, we demonstrate the epidemiological consequences of alternative control policies, showing the incidence of new infections that we note can be very different from the number of detected infections owing to both test sensitivity and spatial patterns of testing.

#### **Table**

<b>Type of Cost</b>	<b>Calculated as:</b>	<b>Reference</b>
<b>Direct Farm Costs (FMD)</b>	$\text{£}1962 \times \text{Culled Cattle} + \text{£}523 \times \text{Culled Sheep}$	[16, 35]
<b>Direct Farm Costs (BTV)</b>	$\text{£}145 \times \text{Infected Cattle} + \text{£}29 \times \text{Infected Sheep} + \text{£}203 \times \text{Sheep Deaths}$	[36]
<b>Direct Farm Costs (bTB)</b>	$\text{£}1557 \times \text{Infected Cattle} + \text{£}531 \times \text{Breakdowns}$	[37]
<b>Welfare Costs</b>	$\text{£}8.00 \times \text{Farm Days Restricted}$	[16, 35]
<b>Agricultural Sector losses</b>	$\text{£}227 \times \text{Animal Movements Prevented}$	[16, 35]
<b>Export Losses (FMD only)</b>	$\text{£}655,000 \times (\text{Duration of Export Ban})$	[16, 35]
<b>Tourism (FMD &amp; BTV)</b>	$\text{£}271 \times \text{Farm Days Restricted}$	[16, 35]
<b>Testing (bTB only)</b>	$\text{£}10 \times \text{Cattle tested}$ (approx $\text{£}2.50$ to farmer and $\text{£}7.50$ for performing the test)	[37]

**TABLE 1.** Costs related to movement bans for the three livestock diseases: Foot-and-Mouth Disease (FMD), Bluetongue Virus (BTV) and bovine Tuberculosis (bTB). All costs have been inflated from the date the assessments were made to generate prices relevant for 2019. Here Farm Days Restricted refers to the number of farms each day that are placed under movement restrictions summed across the epidemic.

## Methods

### The FMD Model

The mathematical model utilised in this paper is a modified version of the FMD model used both during and after the 2001 outbreak by Keeling and co-workers to predict the spread of disease and the impact of control [2, 26]. Infection between farms can occur via two mechanisms – movements of infected livestock and local, distance-dependent transmission. The local transmission component of the model encapsulates the risks associated with aerosol spread, direct contact of infectious and susceptible animals or fomites (i.e. contaminated vehicles or farm equipment). The rate at which an infectious farm  $j$  transmits infection to a susceptible farm  $i$  via local spread is given by:

$$R_{i,j} = \sum_k \sigma_k N_{k,i}^{p_k} \times \sum_l \tau_l N_{l,j}^{q_k} \times K(d_{ij})$$

$\sigma_k$  represents the susceptibility of species  $k$  on susceptible farm  $i$ ,  $\tau_l$  is the transmissibility of species  $l$  on farm  $j$ ,  $N_{k,i}$  is the number of animals of species  $k$  on farm  $i$  and  $p_k$  and  $q_k$  are power-law parameters accounting for a non-linear increase in susceptibility and transmissibility as animal numbers on a farm increase. Previous work has found that this power-law model provides a closer fit to the 2001 data than one in which the powers are set to unity [38-41].  $K(d_{ij})$  is a distance dependent transmission kernel that is estimated from contact tracing data from the 2001 outbreak [2]. In line with previous work [39], all model parameters are estimated for five

distinct regions: Cumbria, Devon, the rest of England (excluding Cumbria and Devon), Wales and Scotland. This allows the model to account for regional variation in FMD epidemiology and animal husbandry.

In order to assess the daily risk of between farm infection occurring via movement of live animals, a movement network ( $A$ ) is integrated into the model, mimicking the impact of animal movements from infected farms. The probability of a susceptible farm  $i$  being infected by an exposed or infectious farm ( $E_j$  or  $I_j$ ) through a live animal movement, is given by:

$$\lambda_i = \sum_j A_{ji}(E_j + I_j)$$

Here  $A_{ji}$  is the daily risk of movement occurring from farm  $j$  to farm  $i$ , calculated by averaging recorded cattle movements across a year; these livestock movement data were obtained from DEFRA and the Scottish Government and have been analysed in a number of studies (e.g. [14, 42-44]). Given our assumptions that infection acts at the level of the entire farm, we are only concerned with batches of livestock movements, not the number of animals in these batches.  $E_j$  and  $I_j$  are indicator variables (0 or 1) which inform about the current status of farm  $j$  in the simulation.

Simulations in this paper are seeded by infecting 5 (randomly chosen) farms in a 5 km cluster (in a randomly chosen location) within a given county to approximate the initial conditions of a localised outbreak; detection of the first case and the implementation of controls then follows. In line with previous work, we assume that all livestock on IPs are culled within 24 hours of being reported and all associated dangerous contacts (DCs) are culled within 48 hours [30]. Contiguous premises (CP) culling is not performed.

In order to determine the effectiveness of a livestock movement ban, we utilise data from the 2001 FMD epidemic that detail the costs associated with the outbreak. The economic costs of the 2001 outbreak fell into 5 distinct categories: direct costs, indirect costs, costs associated with welfare culls, losses to the agricultural sector and losses to tourism [35]. We will utilise this

economic framework to translate our simulation results into a national epidemic cost, although alternative scenarios could be considered, such as minimising the cost to the farming industry or to the UK tax-payer. In 2001 (and 2007) national scale movement bans were imposed such that animals could only be moved under specific veterinary licence. Here we relax this control measure and consider a range of movement bans that act upon all farms within a given radius of infected premises. We impose this radius based on the straight-line distance between the recorded point location (which generally identifies the farmhouse) of each pair of farms; in practise regional control teams would presumably account for the location of livestock, although this distinction is likely to be negligible for large radii. The parameters used in the FMD simulations are taken from matching regional prevalence from simulations to the results of the 2001 FMD outbreak (see Supplementary Table 1).

## **The BTV model**

Our model for BTV operates at the level of individual animals, replicating the known pattern of animal movements and captures the transmission of infection through spatially dispersing midge vectors that are affected by climatic conditions in a similar fashion to other spatial models of BTV transmission [33, 45-47].

The model describes each farm as a stochastic metapopulation of sheep and cattle [33, 45], the two main ruminant hosts of BTV amongst European commercial livestock. The livestock population at each farm  $i$  is subdivided by their species  $k$  and BTV infection status: susceptible ( $S_{k,i}$ ), infected and infectious ( $I_{k,i}$ ) and recovered and immune ( $R_{k,i}$ ). The total population at each farm is assumed to remain static except for movement of infected animals and disease induced mortality. The infectious duration for BTV in a given animal is modelled as a multi-stage Erlang process according to commonly used estimates of BTV viraemia amongst cattle and sheep [48]. *Culicoides* biting midge spatial population dynamics are described using a spatial grid overlaying the UK at a 5 x 5km resolution, therefore each grid might contain 0, 1, 2 or more

farms. The grid cell locations and daily mean temperature for each cell was drawn from the UKCP09 [49] retrospective data for 2007, the year of the first UK BTV outbreak. The midge population in the spatial grid at coordinate location  $x$  is described by a Poisson distribution for the number of latently infected midges ( $E_{M,x}$ ) and actively infectious midges ( $I_{M,x}$ ). The mean of these two distributions is determined by biting on infected livestock within the grid, and by dispersal of infected midges from nearby grids (see below). The latency duration (or extrinsic incubation period) of infected midges is modelled as a 10 stage temperature dependent Erlang process [31, 50].

The daily number of bites emanating from the infectious midges in the grid square at location  $x$  is Poisson distributed with mean  $\alpha(t, x)I_{M,x}$ , where  $\alpha(t, x)$  is the biting rate for midges using the mean daily temperature on day  $t$  at the grid square  $x$  [31, 48]. The expected proportion of all daily infectious bites distributed to a single animal of species  $k$  in farm  $i$  within the spatial grid box at  $x$  is:

$$\phi_{k,i} = \frac{\pi_k (\sum_l \pi_l N_{l,i})^{p-1}}{\sum_{j \in x} (\sum_m \pi_m N_{m,j})^p}.$$

where  $\pi_k$  is the relative preference of midges for species  $k$  and  $p$  is a parameter tuning the seeking preference of midges for larger farms within the grid cell. The sum in the denominator is over all the farms in the grid box at  $x$ . Therefore, the risk of the animal being infected on each day  $t$  is:

$$1 - \exp(-P_H \phi_{k,i} \alpha(t, x) I_{M,x}).$$

where  $P_H$  is the probability of BTV transmission per bite from an infectious midge.

We assume that the expected number of susceptible midges arriving to bite each animal each day is proportional to the expected prediction of a seasonal and temperature dependent generalised linear mixed-effect model (GLMM) inferred from wide-scale midge trapping experiments in the UK and specialised to the activity of *C. Obsoletus* females [31, 51]. Underlying GLMM random effects were drawn either once per simulation for each farm (for farm

level random effects) or daily for each farm (overdispersion and autocorrelation random effects). We denote the unscaled mean biting rate prediction from the GLMM, conditional on local temperature and random effects for each farm on each day  $t$ ,  $B(t, x)$ . Therefore, the expected number of newly infected midges in the grid cell at  $x$  on day  $t$  is:

$$qP_V B(t, x) \sum_{j \in x} \sum_k \pi_k I_{k,j}.$$

Where  $P_V$  is the midge BTV infection probability per bite on an infected host, and  $q$  is a parameter that scales the difference between the biting rate and the trap capture rate.

In line with the known biting behaviour of *Culicoides* midges [52-53] we assume that all biting occurs over short dusk/dawn periods and that otherwise midges are in oogenesis, seeking oviposition sites or seeking new hosts. We model the movement of midges between daily biting as an inhomogeneous diffusion process with the local diffusion rate at each grid square  $x$  as:

$$D(x) = \frac{D_0}{1 + \xi \sum_{j \in x} (\sum_m \pi_m N_{m,j})^p}.$$

where  $D_0$  is the reference diffusivity of midges in a grid square devoid of commercial livestock hosts and  $\xi$  is a tunable scalar. The diffusion rate for the grid box  $x$  depends on the denominator for the proportion of bites per animal; this quantity acts as an effective population size for the grid box. That is, we model diffusion as decreasing with more animals per grid square and higher values of the seeking behaviour parameter.

The daily number of BTV-infected animals introduced into a farm  $i$  due to livestock movement from farm  $j$  was calculated in three steps for each day: 1) for each farm pair a movement was generated with probability  $A_{ji}$  (see above), 2) if a movement occurred in step 1 it was chosen randomly to be a batch of sheep or cattle according the relative population density in the farm sending the batch, 3) a batch size was randomly generated according to species type and infected animals of the chosen species were sampled uniformly without replacement from the total population of the chosen species at the sending farm. Only infected animals were moved

within the simulation, in order to better minimise population flux and in line with other simulation studies of BTV in the UK [33].

The morbidity and mortality rates associated with BTV serotype 8 infection were low during the 2006 outbreak [17]. Therefore, we assume that the introduction of BTV into the UK is initially cryptic (occurring on 1st June) and the virus spreads without movement bans until it is detected by either a) the death of an animal due to disease induced mortality, or b) clinical signs of BTV are detected amongst infected animals. The probability of clinical detection per farm per species per day is:

$$Q_{k,i} = 1 - (1 - p_{D,k})^{I_{k,i}}.$$

where  $p_{D,k}$  is the daily chance of an infected animal of species  $k$  showing clinical signs of BTV. After detection of a BTV outbreak we assume that DEFRA recommendations are followed and all farms within 15km of the initial IP have all their animals investigated for BTV [54]. The initial zones (CZ, PZ and SZ) are constructed around all the detected IPs, and are extended as new IPs are detected during the ongoing outbreak. Parameters used in the BTV model are provided in Supplementary Tables 2 and 3.

## **bTB Model**

In this paper we make use of a national-scale stochastic metapopulation model of bTB transmission and detection [12]. In essence the model operates at the scale of individual farms, but (unlike the FMD model) captures the stochastic cattle-level infection dynamics within a farm; this is necessary as an infected farm is likely to contain only a few infected cattle. Each farm is defined by its location and the number of susceptible, latently infected and infectious cattle present on a given day; sheep, pigs and other livestock species are assumed to have no role in bTB transmission.



The transmission and disease progression processes within the model are stochastic, and occur in discrete time as follows: for farm  $i$  the number of Susceptible, Exposed and Infectious cattle are given by:

$$\begin{aligned} S_i(t+1) &= S_i(t) - \Lambda_{i,t} \\ E_i(t+1) &= E_i(t) + \Lambda_{i,t} - A_{i,t} \\ I_i(t+1) &= I_i(t) + A_{i,t} \end{aligned} \quad \begin{aligned} \Lambda_{i,t} &= \text{Bin}(S_i(t), 1 - \exp(-\lambda_{i,t})) \\ A_{i,t} &= \text{Bin}(E_i(t), \alpha) \end{aligned}$$

where  $\lambda$  is the force of infection acting on cattle within the farm (see below), and  $\alpha$  is the rate at which latent animals become infectious.

In addition there are three deterministic demographic processes acting on the farm – births, deaths and movements – which follow the recorded pattern from the UK's Cattle Tracing System (CTS), which is run by the British Cattle Movement Service (part of the Department for Environment, Food and Rural Affairs, DEFRA). All three of these processes can be considered as a movement; births are movements onto a farm without an origin and deaths are movement from a farm without a destination. For all of these movements, an individual animal is chosen randomly independent of its infection status or its history of movements. The recorded movement of ~30,000 cattle per day is one of the primary mechanisms of long-range transmission of infection from the movement of infected animals.

Transmission to cattle on a given farm comes from three different sources: cattle-to-cattle transmission, transmission from infection within the farm environment and transmission from infection within the wider environment. Hence the force of infection,  $\lambda$ , to cattle on farm  $i$  is given by:

$$\lambda_{i,t} = \beta \frac{I_i(t)}{N_i(t)} + f v_i(t) + F V_i(t)$$

where  $N_i (= S_i + E_i + I_i)$  is the number of cattle on farm  $i$ ,  $v$  is the level of infection in the farm environment, and  $V$  is the level of infection in the wider environment which is considered to be the local parish [12]. The level of infection in the environment is increased by the proportion of infectious cattle, but wanes over time as the bacteria become non-viable.

$$\frac{dv_i}{dt} = \frac{I_i}{N_i} - \epsilon v_i$$

$$\frac{dV_i}{dt} = \frac{\sum_{j \in Parish} I_j}{\sum_{j \in Parish} N_j} - \epsilon V_i$$

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597 These two local reservoirs of infection could both represent the persistence of infectious matter  
598 on pasture or persistence in a local wildlife reservoir.

599 In addition, we simulate routine testing for surveillance, which follows the DEFRA rules  
600 appropriate for the time and varies between annual and 4-yearly testing depending on location.

601 This test is not perfect [55] and we therefore use a test sensitivity of  $\rho$  for infectious cattle and  
602  $\rho_E \times \rho$  for exposed / latent animals. Once infected cattle are detected within a farm, the animals  
603 are culled and the farm placed under movement restrictions until all its cattle clear a further two  
604 tests at 60-day intervals; in addition these farms are also subjected to further testing after 6 and  
605 12 months.

606 The model parameter are inferred by matching simulations to the number of reactors (positive  
607 cattle) and number of failed herd tests recorded per county per year between 1997 and 2007  
608 using Sequential Monte Carlo Approximate Bayesian Computation [12]; the main parameters  
609 are given below.

610 The model was adapted to allow us to investigate the addition of radial movement restrictions.  
611 Given that bTB is an endemic disease (unlike FMD and BTV), movement restrictions must be  
612 temporary with some means in which they are lifted from given farms in the future. In our  
613 adapted model, when a herd is first identified as being infected (that is an animal tests positive  
614 on a farm that is not under restrictions), we assume that movements from the infected farm and  
615 those within a radius of the infected farm are banned. (although we also simulate the extreme  
616 case where there are no movement bans, even on the infected farms). The infected farm is  
617 subject to the usual measures, with the positive animal(s) culled and movement restrictions in

place until two follow-up tests (at 60-day intervals) are all clear; additional tests at both 6 and 12 months are scheduled. For those farms within the radius (which may be considered at risk due to their proximity) movements are banned until a follow-up test after 30 days can be performed – following the results of this test either movements are resumed or the farm is identified as infected and the entire process is repeated. In this way, waves of testing spread through high prevalence areas. Results from such control policies are shown in the main paper.

A modification to this control policy is explored further below. Farms with cattle testing positive are handled as described above; farms within the surrounding radius are only subject to follow-up tests but do not have their cattle movements restricted. This policy is extended to have slightly higher incidence (due to movement of cattle to new regions) but significantly lower economic costs due to the reduction in movement restrictions.

Simulations begin in 1998 and utilise the pattern of recorded movements and random herd-level test; changes to the control policy (additional radial controls and testing) is assumed to begin at the start of 2005, and its impact over 6 years on the progress of the endemic recorded.

## **Methods References**

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